Populations without Reproduction

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For a population to undergo evolution by natural selection, it is assumed that the constituents of the population form parent-offspring lineages, that is, that they must reproduce. I challenge this assumption by dividing the notion of reproduction into two subprocesses, that is, multiplication and inheritance, that produce parent-offspring lineages between the parts of a population, and I show that their population-level roles, generation and memory, respectively, can be effected by processes that do not rely on such local-level lineages. I further argue that these two population-level processes, not local parent-offspring lineages, are necessary conditions for a population to undergo Darwinian evolution.

1. Introduction. A belief shared among evolutionary biologists and philosophers of biology is that for a population to undergo evolution by natural selection, the individuals forming the population must form parent-offspring lineages. Darwin assumed this, and it is also part of the commonly held tripartite conditional scheme of variation, heredity, and fitness differences attributed to Lewontin (1970, 1985). The process that engenders these lineages is commonly held to be reproduction, where (1) an entity produces a new one and (2) the produced entity is similar in some respect to its producer. Both roles establish a lineage between the two concerned entities. In the first case, there is a productive lineage where an entity produces an offspring and therefore is its parent. In the second case, the lineage is one of entities "passing on their traits" or "transmitting some characteristic" to one another, the se-

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quence of such events constituting the lineage of inherited similarity. While both types of lineages are often conflated together, as is the case with reproduction, the recent recognition that there are multiple inheritance systems with asymmetric transmission networks allows us to differentiate them and study there interrelationships (Jablonka and Lamb 2005). However, even when dissociated, both lineage types have been assumed necessary for a population to evolve through natural selection (e.g., Mameli 2004). This assumption has also led some to argue that most cases of supposed cultural transmission do not count as cultural analogs to reproduction since social learning fails more often than not to establish parent-offspring lineages, meaning that cultural change should not be considered as a form of Darwinian cultural evolution (Godfrey-Smith 2009, 2012).

In this paper, I challenge the assumption that parent-offspring lineages are required for any population system to undergo evolution by natural selection. In order to do so, I will divide reproduction into its two component processes producing parent-offspring lineages and examine the role of each in allowing a population to evolve in a Darwinian manner.[1] I will argue that it is their population-level effects that are really necessary for a population system to undergo Darwinian evolution and that a multitude of local-level processes can ensure these roles, not all of which involve parent-offspring lineages. This means that parent-offspring lineages between the constituents of a population are but one means among others to ensure that the population itself evolves by natural selection. It also means that the lack of clear parent-offspring lineages in social learning is not in principle an impediment for culture to undergo Darwinian evolution.

Key to my argument is the distinction between local-level and population-level roles of processes. By local-level roles, I will refer to the processes and events concerning the actions and interactions of individuals whether or not they are part of a population. Differently put, a local-level process concerns what happens in an individual's life. Organisms live and die, eat and get eaten, copulate and give birth, divide and grow, and so on. In this sense, parent-offspring relationships are local-level, and so is reproduction, since both concern individual biographies.

By population-level roles, I will refer to the processes and events taking place at the level of the population system through the agglomeration of local-level processes and/or events. Resource scarcity by overpopulation is

1. The analysis of reproduction made here does not pretend to be exhaustive. Since the argument concerns transgenerational relationships and not intragenerational ones, developmental aspects of reproduction will be largely put aside. While development is a major part of reproduction, questions of the interrelationships between development, multiplication, and inheritance have no immediate impacts on the problem examined here.

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such an event: only when considering a population with resource-consuming constituents can there be scarcity of resources in a given environment. Two wolves fighting over a lump of meat compete against one another in a local-level interaction, but it only leads to a population-level Malthusian struggle for existence if resources are scarce and competitive interactions are generalized throughout the population.

Darwinian evolution itself is a population-level phenomenon. Understood broadly, evolution is a transgenerational change in the relative frequency of variants in a population. Darwinian evolution is evolution effected by natural selection. The change in distribution can be due to local-level processes, but the change itself is an ongoing process at the level of the population since it is obtained through the agglomerations of local-level events impacting the population system's properties (distribution of variation).

The distinction is not a plea for a specific form of population-level causation (e.g., Millstein 2006). I will assume throughout the discussion that populations are integrated causal systems (Millstein 2009, 2010, who prefers to call them 'individuals');[2] the nuance should be understood as a form of scaling up from the level of individuals' activities to their results on the population system of which they are a part. Whether or not there can be population-level causation does not affect the argument.

The two local-level processes I will examine here are multiplication and inheritance. I will argue that it is their population-level effects, generation and memory, respectively, that are necessary for a population system to undergo evolution by natural selection and that multiplication and inheritance can ensure these population-level conditions without forming parent-offspring lineages. I will show that there are local-level processes that do not form local-level lineages but that could nevertheless confer a population the capability to evolve by natural selection.

2. Multiplication

2.1. Local-Level Multiplication. By 'multiplication' I refer to a *process where one or many entities or processes produce or participate in the production of a new entity of the relevant kind*. What serves as the relevant kind is that the newly produced entities all share a common property slot (trait type) that can have the same value (eye color, number of limbs, etc.). Multiplication does not require variation in the value that the relevant trait type

2. Although I will not adopt any specific definition of what counts as a population system, the present discussion makes it clear that reproduction or lineages between population parts are not necessary for a grouping of individuals to count as a population system (although they may participate in increasing the population's causal cohesiveness). Other forms of interactions, such as ecological interactions, may suffice for groupings of individuals to serve as population systems with evolutionary capabilities.

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takes (e.g., brown or blue eyes, six or four limbs), only that the newly produced entities have a common trait type. However, it must allow for variation if the population of multiplying entities is to evolve. This mirrors Mameli's (2005) notion of inheritance of variation for a trait where a dimension of similarity is inherited, but with the difference that no parent-offspring relationships are presumed here. I will reserve the transmission of specific trait values (of variation per se) for the inheritance process.

Multiplication as a subprocess of reproduction engenders lineages between the producer and its offspring. The parents are producers of their offspring, and if these products are apt themselves to multiply, the lineage can persist indefinitely. Moreover, in standard accounts of reproduction, the producing entities are themselves of the same relevant kind as their products, their offspring, and excluding cases of migration, the producer is also part of the same population system as its offspring.

However, note that the process of multiplication spelled out here is larger than the way it is realized in reproduction. Multiplication does not presuppose sameness of kind between producers and products or that they should be part of the same population system. For instance, translation is a process of protein multiplication even though ribosomes and mRNA are not themselves proteins. Neither does multiplication entail parent-offspring lineages (see below). Moreover, no specifically biological process or entities are required. This greater generality allows nonbiological cases of multiplication, such as when a rock breaks into two smaller rocks.

Nevertheless, this notion of multiplication (with or without lineage) does offer some constraints on what can and what cannot multiply. For one thing, it assumes that we can count and differentiate both the producer and the product since the product must be a new entity (or individual). Fire hardly multiplies since it is not obvious what counts as a new fire unit, although one burning house igniting another may count as multiplication of burning houses. For multiplication with lineage, this is important because the number of products through multiplication can then be understood as the number of offspring that a parent produces, so that multiplication numbers are what we count when we measure the realized fitness of organisms or genes. However, deciding what to count and how to count it are problems that go beyond the scope of this analysis.

2.2. Population-Level Generation. What role does multiplication play in evolution? Not all multiplication processes lead to evolution, but those that do so ensure that population parts are regenerated as older ones are destroyed. Multiplication produces, at the level of the population, both a renewal of population parts and a time frame to differentiate developmental changes from evolutionary changes. This dual population-level role assumed by multiplication I will term here 'generation'.

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Multiplication ensures a renewal of population parts and thus ensures the persistence of the population system. Without multiplication, the loss of population constituents means that the population will diminish in part numbers, and in time the population will simply shrink away. A population can persist as a historical individual although all of its parts are being continuously replaced.

Multiplication is also a generation marker. Older and younger population constituents are part of different generations, and it is the episodes of multiplication that distinguish generations. This is important because intragenerational change does not count as evolution. The mean increase in size of the population constituents may be simply due to individuals growing as part of their normal development. Generations need not be discrete (they can overlap), but for evolution to occur, the change in the distribution of variants must be transgenerational.

2.3. Multiplication without Lineage. The formation of local-level lineages is not a necessary condition for a multiplication process to ensure generation at the level of the population. Parent-offspring lineages are but one way to ensure population continuity through the renewal of parts. As long as new parts of the same relevant kind are formed and integrated into the population system, there is no need for these parts to be related by lineage. There are many empirical cases—where generation is ensured through multiplication without lineages—that can illustrate this. Prions are a good example of this.

Prions are the infectious proteins responsible for spongiform encephalophaties such as mad cow disease. These misfolded proteins can convert functional cellular proteins with the same amino acid sequence into adopting their conformation (general three-dimensional shape or folding; Prusiner 1999). While the precise mechanisms by which conversion proceeds are still debated, a template transmission process is often assumed (Shorter and Lindquist 2005). According to this hypothesis, the 'normal' cellular protein (either folded in its functional state or in a transiently unfolded state) is recruited by an agglomeration of prions (forming amyloid sticks), which then misfolds the protein into the prion form. While prions can transmit their conformation to other proteins, the converted proteins are products of mRNA translation. Protein multiplication thus occurs without the normal cellular protein or the prion participating in their material production. Inhibiting the gene responsible for the protein terminates prion conversion since prions depend on prior proteins to transmit their form (Chien, Weissman, and DePace 2004). Prions can also come in many variant strains differing both in their conformational structure and in their intra- and extracellular phenotypic effects. It has been argued that these strains can compete against one another and the normal cellular form, a competition leading to a process of Dar-

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winian evolution of these strains (Li et al. 2010). So populations of prions can in principle evolve through natural selection even though they do not form parent-offspring lineages when multiplying.

However, it has been claimed that even though prions do not produce new proteins, they still reproduce. Godfrey-Smith (2009, 79–81) construes prion conversion as a case of 'formal reproduction', where a parent entity does not materially contribute to the production of a new individual but where there is still a discernible parent-offspring relationship between two entities. The lineage is established by a process of trait transmission (the conformation in the case of prions), the sender being the parent and the receiver being the offspring. So, according to this line of thought, reproduction is still a necessary local-level condition for a population to undergo Darwinian evolution since inheritance requires a parent-offspring relationship, and that is what reproduction is minimally all about. I will now argue against this view by showing that not all inheritance mechanisms need to rely on a local-level parent-offspring relationship while still allowing the population system to evolve by natural selection.

3. Inheritance

3.1. Local-Level Inheritance. The received view of inheritance has it that an organism resembles its parent(s) because of the genetic material its parent transmitted to it. This claim is being more and more challenged by the multi-systemic view of inheritance according to which there are other means of inheritance than genetic transfer (e.g., Mameli 2004; Jablonka and Lamb 2005). This alternative view of inheritance shares with Godfrey-Smith's (2009) formal reproduction concept the idea that inheritance systems are mechanisms that ensure parent-offspring similarity and thus depends on parent-offspring lineages. Lewontin (1985, 76) calls this "the principle of heredity."

According to the multi-systemists, inheritance is a process through which an entity (a 'parent') affects another entity (its 'offspring') in such a way that the offspring resembles more its parent with regard to the transmitted trait than it does the other constituents of the population (Mameli 2004). For instance, with cultural inheritance, teachers count as "cultural parents" of their pupils, their "cultural offspring," even if biologically unrelated (Boyd and Richerson 1985). An inheritance system is thus conceived as a mechanism that ensures a parent-offspring similarity with regard to a specific trait.

Note that this does not mean that the 'inheritance' offspring is a material product of its 'inheritance' parent. Productive relationships concern multiplication, not inheritance, so that with a multi-systemic view of inheritance systems, inheritance lineages may differ from multiplication ones in their network structures. With horizontal or lateral transmission, the inheritance lineage network of a population does not superimpose on the multiplication

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lineage (which is by default vertical), so that individuals of the same generation can transmit traits to one another, and younger individuals can even transmit traits to older ones, while this is logically excluded for multiplication lineages.

3.2. Memory. What does parent-offspring similarity do when it comes to allowing a population system to evolve by natural selection? Otherwise put, why is parent-offspring similarity so important (deemed necessary) for evolutionary matters? A reason is given by Lewontin (1985) when he examines why his tripartite scheme requires that offspring resemble their parents. After having equated parent-offspring similarity to the idea of heritable variation, Lewontin claims that "the existence of heritable variation is especially crucial. If variation exists but is not passed from parent to offspring, then the differential reproductive success of different forms is irrelevant, since all forms will produce the same distribution of types in the next generation" (1985, 76).

Key to Lewontin's rationale is the scaling up of local similarity between parents and offspring to properties of the population itself, that is, the distribution of variation of population constituents. Inheritance is necessary because it ensures that variation is preserved from one generation to the next. However, mere transgenerational similarity is not enough. If for every generation there is a random redistribution of variation, we can expect some transgenerational stability in the distribution of variation but no room for cumulative evolution. What matters is that a change in the distribution of variation of a generation is preserved from one generation to the next. For selection to lead to cumulative adaptation, its marks on the population system must be preserved. It goes the same for other evolutionary mechanisms (e.g., mutation, migration, and drift). So by 'memory' I will mean the *process of transgenerational retention of change in the distribution of variation of a population system*, with inheritance systems being those local-level mechanisms the agglomeration of which effects the retention.

Lewontin suggests, as I believe most would, that if there is no parent-offspring similarity, a change in the distribution of variation due to natural selection would not be passed on to the next generation, and so no cumulative adaption could obtain. The justification goes as follows: If A variants are better adapted than B variants in surviving to a mature stage, then the relative frequency of As that reached maturity will probably have increased, whereas Bs will have decreased. Inheritance through parent-offspring similarity ensures that the change occasioned by natural selection will be passed on to the next generation since there will be more As transmitting their trait value and less Bs to do so. The change in proportion of parent variants will be reflected in the distribution of offspring trait values, assuming that fecundity is independent of the trait value.

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This standard explanation is correct in that it shows why parent-offspring similarity is apt to ensure memory. However, such an explanation gives no justification as for the necessity of reproduction or local-level lineages, that is, it is not explained why mechanisms that do not produce lineages cannot also ensure memory. To better understand why parent-offspring similarity is not a necessary condition for memory, it will prove useful to examine the problem through the idea that the population distribution in variation is encoded and transmitted from one generation to the next.

Inheritance systems, through their agglomerated local-level effects, ensure that the later generation's variation distribution is an image of the earlier one. The way parent-offspring similarity ensures this population-level similarity can be likened to a form of digital memory where every parent of the earlier generation serves as one unit of information, the value of which is the individual's specific trait value. The following generation's variation distribution is then produced by mapping all of its constitutive units onto those of the earlier generation (assuming that there is no migration) and by making all such matched pairs have the same value (assuming perfect inheritance). Reproduction ensures this mapping process by the parental unit directly transferring its trait value to its offspring (through material transfer of the genetic material, or by other epigenetic means). In this way, an image of the earlier generation's variation distribution is redrawn onto the later one. Of course, errors can occur, and this may fuel cumulative evolution.

Such a digital memory system, where all parcels of the information concerning the population's statistical distribution are preserved through local interactions of the population's parts from one generation to the next, is a good solution for securing the capability for the population system to undergo Darwinian evolution. However, there is nothing in the concept of memory that necessitates such a digital system with a strict local-level mapping. All the memory process requires to be realized is that the constituents of the population interact in such a way that the variation distribution and its changes due to evolutionary mechanisms be retained from one generation to the next. Such a role is completely defined at the level of the population without reference to any specific local mechanisms.

In the remainder of this paper, I identify a set of conditions that, if satisfied, would allow a population system to undergo Darwinian evolution while being devoid of inheritance with lineage. These conditions are not necessary ones, but they do offer a sketch of a system where the information about the earlier generation's distribution of variation is encoded and transmitted as a whole and not as a series of discrete values, thus bypassing the requirement of local-level inheritance lineages.

3.3. Inheritance without Lineage. Imagine that an experimenter is working with a laboratory population of bacteria that possesses a certain dis-

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tribution of variation for some trait type. For matters of simplicity, we will assume that the bacteria are artificially synthesized by the experimenter so that they do not multiply on their own. The experimenter introduces some chemical compound in the local environment of the experimental population, which has as an effect to kill different bacteria variants in larger proportions than others. Otherwise put, some variants are more resistant to the chemical compound than others. After having introduced the compound and waited for a specified amount of time, the experimenter counts the number of remaining bacteria of each kind and inputs all this information into a spreadsheet program, which in turn calculates the relative frequency of each kind. Having these relative numbers, the experimenter then synthesizes new ones so that the population regains its size at the beginning of the experiment. The new bacteria are introduced in the artificial environment of their predecessors, but preceding the introduction the experimenter will confer each individual bacterium a specific value for the studied trait type (e.g., through gene insertion). The experimenter uses the following recipe to do so: for each bacterium, the probability that a specific trait value will be inserted is equal to the relative frequency of that trait value in the previous generation, as was computed by the spreadsheet program. The same experimental protocol is repeated for an indefinite number of generations.

The end result of the experiment is that any trait variant that is more resistant to the chemical compound will come to dominate the artificial population system. As with a natural population where the bacteria would have undergone reproduction without external intervention, the selection process will have driven the population to adaptation. However, in the experimental case described above, there are no inheritance lineages between members of the earlier generation and the ones of the following generation. The parent-offspring relationship is lost because the individual contributions of the constituents of the earlier generation are fused in the computation of the relative frequencies of each variant type. This conflation makes any single individual's contribution indiscernible from another's. If Darwinian evolution is a product of natural selection on a population system with variation, generation, and memory, then the experimenter's case is as much Darwinian as the natural population one.

This thought experiment offers a proof of principle of how inheritance without lineage can ensure the capability for a population system to undergo Darwinian evolution. First, the distribution in variation of an earlier generation must be encoded in the state of a system external to the population. With the spreadsheet program, the distribution was encoded in computed numbers representing the relative frequencies of the different variants. Second, the encoded information must be redistributed into the following generation, that is, it must affect the following generation's distribution of variation in such a way that the two distributions are similar. With the experimenter's case, the

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chance setting for trait attribution ensured this condition. Third, along the way of the two previous steps, the individual trait value of any members of the earlier generation must be conflated with the others so that the specifics of any individual contribution to the next generation's variation distribution are lost. With the experimenter's case, this condition was ensured both by conflating individual trait values into relative frequencies and through the chance setting used to redistribute trait values. With the satisfaction of these three conditions, we obtain a memory system where it is the statistical state of an earlier generation that is encoded and then transmitted to the next generation, not the individual trait values themselves. Through such a form of encoding and redistribution, specific parent-offspring relationships are lost, but the end result is the same: there is memory in the population system so that, if a selection process acts, there is a transgenerational retention of the change in variation distribution.

In the thought experiment, intelligence conspires to prevent the population constituents from forming local-level multiplication and inheritance lineages. One sensible way to make the artificial example more credible from a biological point of view is to show that all intelligent interventions of the experimenter can be replaced with known naturally occurring phenomena. This is a familiar strategy: use an artificial case of a process and show by analogy that known unintelligent and naturally occurring processes can replace intelligent interventions by effecting the same results.

Diffused ecological inheritance can satisfy this role. Ecological inheritance is understood here as a family of processes through which developmental resources external to the organisms (or, more generally, to population constituents) are passed on recurrently from one generation to the next, thus actively participating in the transmission of traits of the population's constituents.[3] 'Diffused ecological inheritance' can be understood as a process of ecological inheritance where (1) the state of the earlier generation is encoded in some global environmental state and (2) the environmental state so encoded ensures that the following generation's constituents develop differentially so that a distribution in variation similar to the previous generation obtains. These two conditions can both be satisfied by known naturally occurring phenomena, although I know of no empirical research examining cases where both conditions are satisfied at the same time.

It is rather straightforward how the statistical distribution of some trait variants can affect an environmental state so that it reflects the state of the population. Many species of fish release steroids in their watery milieu (Scott and Ellis 2007). The specific kind of steroid released can be related

3. The way ecological inheritance is defined here differs from in Odling-Smee (2010) in that it focuses on trait variation rather than on the inheritance of changes in selective pressures. My use of ecological inheritance does not require niche inheritance.

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to a specific variant type among the population, such as a specific sex, and so the relative sex-specific steroid concentration in the milieu can reflect the ratio of the steroid-producing variant. For instance, males and females of the common dentex (*Dentex dentex*) release different steroids in the water, and it has been shown that the sex-specific steroid concentrations vary according to the relative frequency of both sexes (Pavlidis, Greenwood, and Scott 2004). Many other environmental states could be influenced in an analogous way, such as mean temperature, pH level, humidity, and oxygenation level. Other collective patterns, such as trail marking, can also serve as a population's imprint on the environment. As long as different variants affect the environmental state differently, the environment has the capacity to encode a generation's distribution in variation for a trait type.

For diffused ecological inheritance to obtain, the environmental state produced by an earlier generation must also affect the development of the following generation so that they share a similar distribution in variation. Developmental plasticity is a ubiquitous phenomenon, making the environment an important determiner of the variation a population exhibits. The diffused environmental states mentioned above are all known to affect the development of traits. Steroid concentrations and mean temperature are known to affect sex determination in many fish (Devlin and Nagahama 2002) and reptile species (Crain and Guillette 1998). Levels of pH are known to affect the way proteins will fold and the structure prion amyloids take (Chien et al. 2004). See Gilbert and Epel (2009) for many more examples.

However, the transgenerational redistribution of variation of an earlier generation is not entailed simply by the fact that populations affect the environment and that the environment affects the population back. The environment must ensure a positive correlation of a trait's relative frequency from one generation to the next. With steroid level and sex determination mechanisms in fish, a negative correlation obtains, so that the more male steroids there are, the more females develop in the new generation. Nonetheless, one can easily imagine cases where a positive correlation would obtain, showing the empirical plausibility of diffused ecological inheritance. Let us go back to prion strains and examine how they could transmit their conformational variation without forming parent-offspring inheritance lineages.

Suppose that instead of converting already-formed proteins through template conversion, prions incapacitate the chaperone molecules responsible for correctly folding the cellular form of the protein. Among other functions, chaperone molecules (such as heat shock proteins) assist in the proper folding of proteins into their cellular forms and prevent undesirable protein agglomerations (Fink 1999). In our hypothetical case, the more prions that are present, the less functional chaperones there will be, either by destroying or by incapacitating them (by augmenting the local pH level, for instance). The diminution in density of functional chaperones will be proportional to the

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number of prions present in the cell, so that a newly formed unfolded protein's probability to misfold into the prion conformation proportionally increases. Differently put, the more prions there are, the less chaperone molecules there will be, so that newly produced proteins will have a better chance of misfolding. If the numbers are right, this process will lead to a stable retention of the relative frequencies of cellular forms and prion forms (or of different prion strains). This means that a change in the relative distribution of cellular proteins and variant prion strains will be retained, thus opening the possibility that Darwinian evolution of prion strains takes place without prions forming inheritance lineages. In this case, inheritance is diffused because prions do not directly act on cellular proteins through template transmission (or formal reproduction), such that parent-offspring relationships cannot be established at the local level. Rather, the transmission goes through the environment by affecting a diffused state (chaperone density) to reflect the relative frequencies of the prions. This environmental change in turn ensures the redistribution of the prion variant forms from one generation to the next since newly produced unfolded proteins are converted accordingly, although indirectly by not meeting a chaperone molecule. No individual prion is responsible for a newly formed prion's conformation. It is the distribution in variation of the population system that gets transmitted from generation to generation.

4. Conclusion. The assumption that parent-offspring lineages are required for population systems to undergo Darwinian evolution is widespread (Lewontin 1970, 1985; Godfrey-Smith 2009). In this paper I have argued that this assumption is incorrect. Local-level lineages participate in two local-level roles, multiplication and inheritance, the evolutionary effects of which are set at the level of the population, generation and memory, respectively. For a population to undergo Darwinian evolution, its parts must be renewed, thus ensuring generational change (the generation condition), and changes in the variational distribution of its parts must be retained from one generation to the next (the memory condition). The mistake is to assume that only reproduction, that is, multiplication and/or inheritance with local-level lineages, can effect these population-level conditions. Although it is recognized that some systems do undergo Darwinian evolution without the help of multiplication lineages, inheritance lineages are still deemed necessary (Mameli 2004; Jablonka and Lamb 2005; Godfrey-Smith 2009). Against this last claim, I have offered an empirically plausible inheritance mechanism, diffused ecological inheritance, apt to bypass local-level inheritance lineages altogether, and have shown that there is at least one plausible way by which population systems can lack any form of local-level lineages. The occurrence of this new type of inheritance can be investigated empirically and the conditions for such

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a form of diffused inheritance to sustain cumulative adaptations through an evolvable population system examined.

Moreover, I have shown that it is a logical possibility that any Darwinian system can evolve without actually forming parent-offspring inheritance lineages. Generation and memory are defined without reference to a specifically biological ontology of entities and processes, so that the same conclusion can be drawn for extra-biological cases of Darwinian evolution, such as cultural evolution. This means that marginalizing or dismissing Darwinian cultural evolution on the grounds that social learning seldom produces parent-offspring lineages (Godfrey-Smith 2009, 2012) is unsound. For instance, cultural transmission could go through a diffused ecological inheritance system. Humans are masters in enriching their environment with knowledge through spatial planning, artifact creations, and institutional organization (Sterelny 2012). Such information-rich environments are potential candidates of diffused ecological inheritance leading to cumulative adaptation. Although this is an empirical problem that goes beyond the scope of this paper, the argument defended here opens the door for further investigation of the occurrence and workings of such diffused inheritance systems.

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